UNDER THE INFLUENCE: WEBS AND BUILDING BEHAVIOR OF *PLESIOMETA ARGYRA* (ARANEAE, TETRAGNATHIDAE) WHEN PARASITIZED BY *HYMENOEPIMECIS ARGYRAPHAGA* (HYMENOPTERA, ICHNEUMONIDAE)

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ABSTRACT. On the evening that it will kill its host, the orb-weaving spider *Plesiometa argyra,* the larva of the ichneumonid wasp *Hymenoepimecis argyraphaga* induces the spider to perform highly stereotyped construction behavior and build an otherwise unique "cocoon web" that is particularly well-designed to support the wasp larva's cocoon. Cocoon web construction behavior is nearly identical with the early steps in one subroutine of normal orb construction, and is repeated over and over. Usually all other normal orb construction behavior patterns are completely or nearly completely repressed. Experimental removal of the larva one or a few hours before cocoon construction would normally occur is sometimes followed by nearly normal cocoon web construction, and sometimes by construction of other highly altered web designs. The mechanism by which the larva induces these changes in the spider's behavior is thus apparently a fast-acting chemical, with effects that are manifested gradually. Partial recovery of orb designs sometimes occurred several days later.

Keywords: Parasite, manipulation of host behavior, orb construction behavior, *Plesiometa, Hymenoepimecis*

Manipulation of host behavior by parasites is a widespread phenomenon (Holmes & Bethel 1972; Moore 1984; Barnard & Behnke 1990; Toft et al. 1991; Godfray 1994; McLachlin 1999; Poulin 2000), but most reports of behavioral modifications, especially those caused by insect parasitoids in other insects, involve only simple behavior patterns such as movement from one habitat to another, adoption of sleeping postures, or eating more or less (Wickler 1976; Godfray 1994; McLachlan 1999). Spider behavior is also influenced by insect parasitoids (Schlinger 1987). At least some of these changes may be due to relatively simple mechanisms, such as modification of particular receptors (Jenni et al. 1980). This report concerns an unusually selective behavioral modification by the larva of the parasitoid wasp *Hymenoepimecis argyraphaga* Gauld (Ichneumonidae), which apparently chemically induces expression of the early steps of one subroutine of orb web construction in the spider *Plesiometa argyra* (Walckenaer 1841) (Tetragnathidae), while suppressing all the rest of orb construction behavior (Eberhard 2000a). It may be the most finely directed alteration of host behavior ever attributed to an insect parasitoid.

It has long been known that psychotropic substances can modify the forms of orb webs (Witt et al. 1968), but the details of how particular steps of the spider's construction behavior are affected have never been determined. Elucidation of which aspects of behavior are changed can have important consequences for the common use of details of building behavior as taxonomic characters (Eberhard 1982; Hormiga et al. 1995; Griswold et al. 1998), as well as how evolutionary transitions may have occurred. It has not always been clear whether or not some variant behavior patterns should be recognized as separate traits (Eberhard 1990). If particular behavior patterns can be selectively induced, then the case for their independence from other traits, and thus their potential usefulness as characters, is strengthened. Clarification of the behavioral effects of this wasp parasite on web construction behavior thus promises to improve understanding of the organization of behavior within the spider, and of the usefulness of different behavioral characters in spider taxonomy.

The life cycle of *H. argyraphaga* is the following (Eberhard 2000b). The female wasp attacks *P. argyra* as the spider rests at the hub of its orb, stings it into a temporary (10–15 min.) paralysis, and glues an egg to the spider's abdomen. Subsequently the spider resumes normal activity, and builds apparently normal orbs to capture prey during the next approximately 7–14 days while the wasp's egg hatches and the larva grows. The larva remains attached to the surface of the abdomen, and feeds by sucking hemolymph through small holes it makes in the spider's abdominal cuticle. The second instar larva, on the night that it will kill its host, induces the spider to construct an otherwise unique "cocoon web" of dragline silk, molts to the third instar, and then kills and consumes the spider. The next evening the larva spins a cocoon hanging by a line from the cocoon web. The larva (which is barely visible through the thin walls of the cocoon) pupates about 4 days later, and then emerges as an adult wasp after about 7 more days.

Figure 1.—Web of an unparasitized adult *Plesiometa argyra*. Scale bar = 3.0 cm.

METHODS

Field observations were made near Parrita, Puntarenas Province, Costa Rica (elev. 10 m) in January and February of 1999 and 2000 in a mature plantation of African oil palm (*Elaeis guineensis* L.) where spider populations were dense. Web measurements were performed in the morning, and thus did not include webs built later in the day (which may have different designs—Eberhard 1988). Construction of cocoon webs made by spiders carrying wasp larvae was observed indoors near Parrita the night after the spiders were collected and transferred onto silk lines from *P. argyra* orbs that had been fastened to approximately horizontal 0.6 m dia. circular wire frames that were hung about 1 m above the floor. Larvae, which would kill their hosts that evening, could be reliably distinguished (15 of 15 cases) from others on the morning and afternoon of the same day, due to their larger size. Voucher specimens of wasps and spiders have been deposited in the U. S. National Museum of Natural History, the Museum of Comparative Zoology at Harvard, and the Museo de Entomología of the Universidad de Costa Rica.

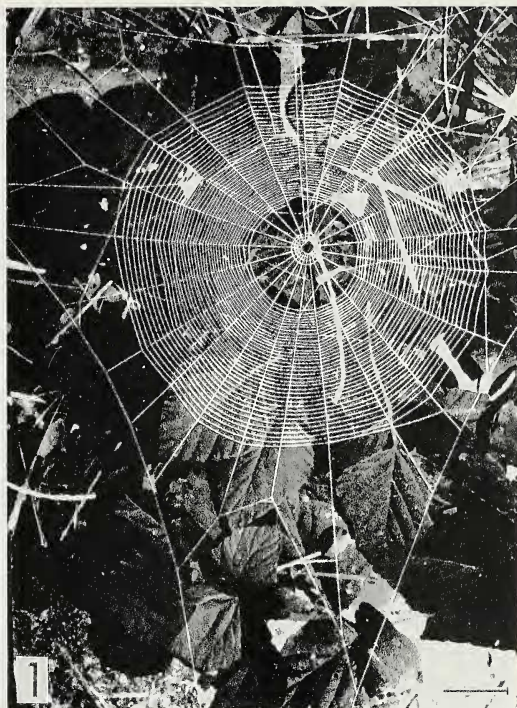The behavior of spiders from which the larva had been experimentally removed was observed after the spiders had been taken to San Antonio de Escazu (elev. 1300 m), where they were kept indoors at room temperature for up to two weeks. On the evening the larva was to be removed, the spider was kept in a small container (6 cm dia.) in which it could not spin a web, and then placed on a wire frame as soon as the larva was removed between 2100 and 0200 h. Because the spiders seemed to need air movement to induce web construction, they were not kept in cages, but allowed to range freely in rooms.

RESULTS

Field.—The orbs of spiders carrying wasp eggs and larvae were not distinguishable from the more or less horizontal, moderately open-meshed orbs of unparasitized spiders (Figs. 1, 2) (ANCOVA analyses showed no significant effects of parasitism by larvae, or by eggs and larvae ($P = 0.91, 0.40$). Even parasitized spiders found the morning of the day on which they would be killed by the wasp larva were on freshly made, apparently normal orbs. Other than orbs, the only other webs on which unparasitized spiders occurred were small molting webs (Eberhard et al. 1993). These
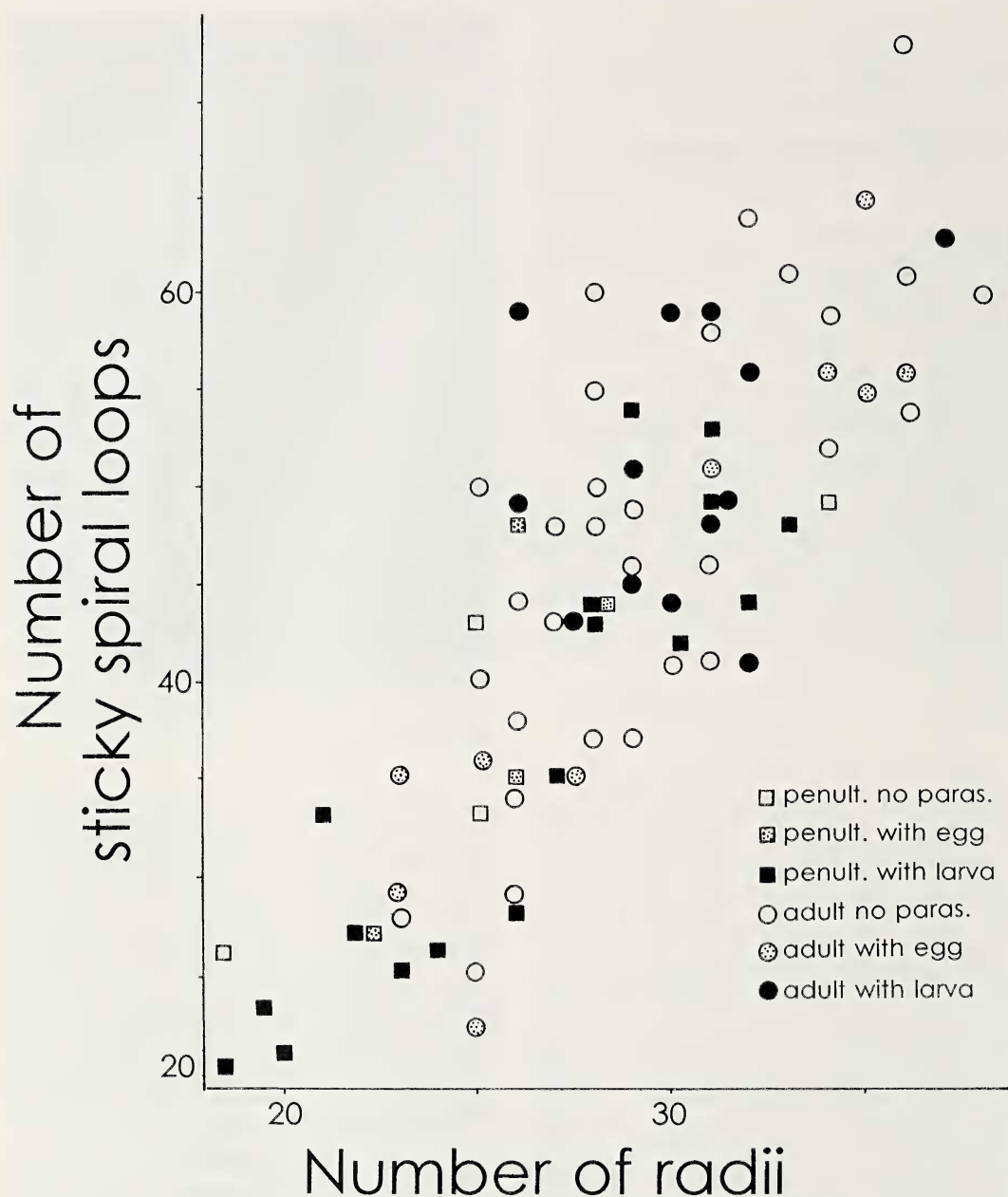
Figure 2.—Numbers of radii and sticky spiral loops (mean number of loops directly above, below, and to the sides of hub) in webs of spiders in the field that were parasitized (filled symbols) and unparasitized (open symbols). No differences between parasitized and unparasitized individuals were apparent.

webs were rare, and several newly molted individuals lacked such webs. Despite the dense spider populations, no egg sacs or webs associated with egg sacs were seen; egg sacs may be hidden in leaf litter, as in the closely related *Leucauge mariana* (Keyserling) (Ibarra et al. 1991; V. Mendez pers. comm.).

More than 100 cocoon webs were observed in the field. They almost always consisted of a few lines that radiated in a more or less horizontal plane from a "hub" or central area, where the cocoon's suspension line was attached, and were each attached directly to a support (Eberhard 2000a, Figs. 3–5). Most ra-
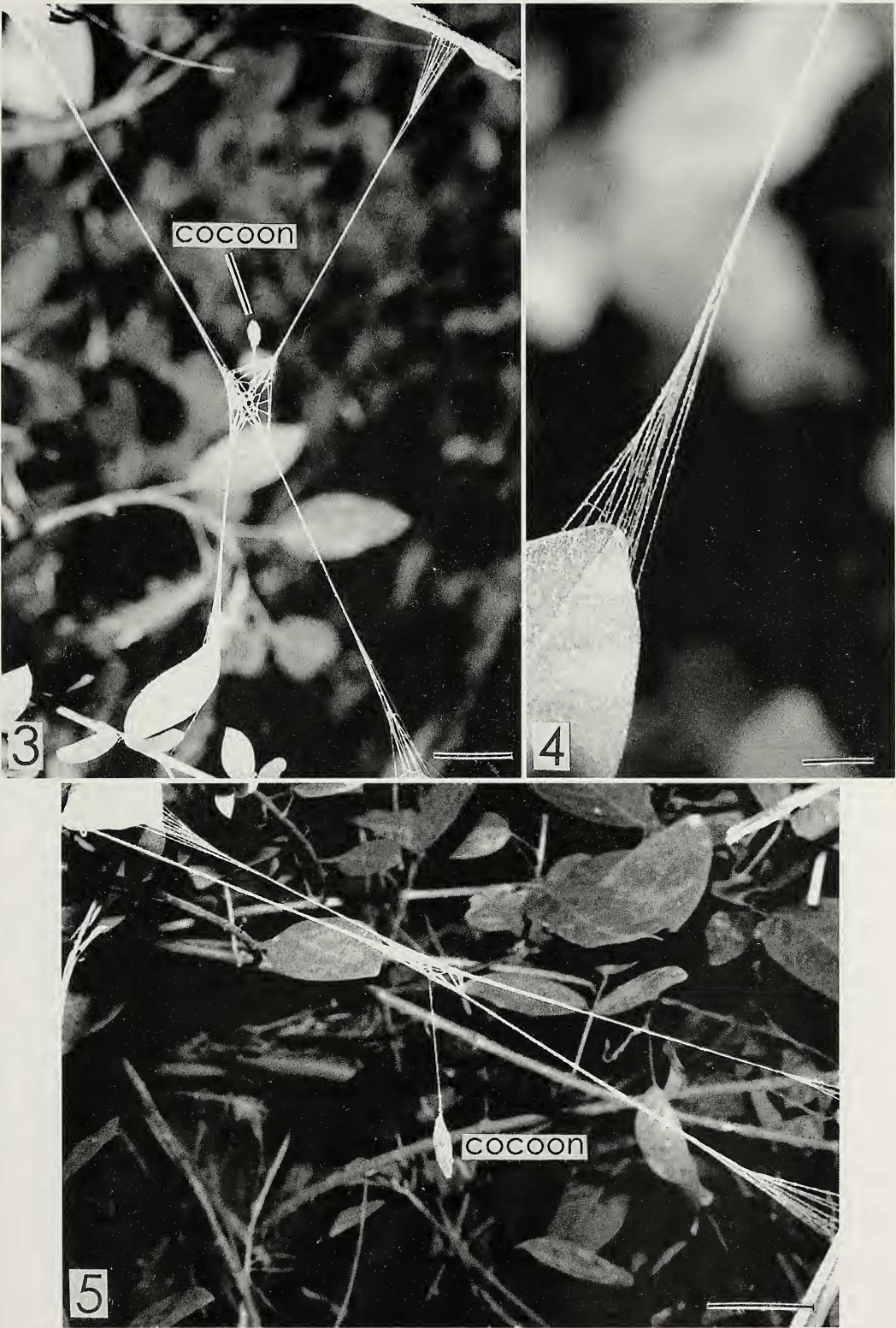
Figures 3–5.—Typical cocoon web. 3. Dorsal view. Scale bar = 3.0 cm; 4. Detail of attachments to a leaf. Scale bar = 0.5 cm; 5. Lateral view. Scale bar = 3.0 cm.

dial lines had many branches near their tips and were thus attached at many adjacent points to the substrate (Fig. 4). They were also sometimes attached at multiple points in the central area. There were several other indications, in addition to the planar arrangement of radial lines, that the webs from which cocoons were suspended represented modified orbs. Some cocoon webs had circular lines similar to those at the hubs of normal orbs (17% of 41 webs checked for this detail) (Figs. 6, 7), though in no case was the central portion of the hub empty, as in normal orbs. Some had one or more frame lines connecting the radial lines (29% of 42 webs checked for this detail) (Fig. 6). These frames were typically much shorter and nearer the hub than were the frame lines of normal orbs (Fig. 1). The most elaborate cocoon web had a distinct hub, frame lines, and a mesh above and below the hub. At the opposite extreme, the two simplest cocoon webs consisted of a single strong line with the larva or the cocoon hanging from the central portion.

Cocoon webs spanned smaller spaces than normal orbs of mature females. The distance between the two most distant points of attachment of anchor lines was smaller in cocoon webs (mean 36.6 ± 17.2 cm in a sample of 38) than in orbs (99.6 ± 47.5 cm in a sample of 31) ($P < 0.001$ with Mann Whitney U-Test). These cocoon webs also had fewer anchor lines (lines directed to the substrate) (mean 3.9 ± 1.5 for cocoon webs, 5.3 ± 1.7 for the orbs; $P < 0.001$ with Mann-Whitney U-Test).

Construction behavior.—Cocoon web construction behavior, observed in five spiders captured in the field the same day with larvae and a sixth three days after being collected, was very consistent. Early in the evening, the spider built several lines, repeatedly removing and shifting the points of attachment as typically occurs during the preliminaries of orb construction of many species of orb weavers (Tilquin 1942; Eberhard 1990). It then remained more or less immobile until between 23:30 and 01:00, when construction activity occurred in bursts. Typically the spider added one to several radial lines in quick succession, and then spent a minute or more (up to 30 min) immobile at the hub before the next burst of activity. The spider's movements showed no signs of weakness or vacillation, and it

moved directly from one attachment to the next as in normal frame and radius construction.

Radial lines were all in nearly the same plane and were added to the web using two similar, simple behavior patterns (Fig. 8, A and B). The spider began by attaching its dragline at the hub, then walked toward the substrate along a radial line, walked along the substrate a short distance and attached the line it had laid from the hub (A_1, B_1). Then it returned to the hub, laying a second dragline as it walked along this line or another radial line that it had laid previously and attached it at the hub (A_2, B_2). When the substrate was thin (a strand of wire, for instance) the spider usually moved to the opposite side to make the attachment before returning to the hub, as is typical of frame construction in orbs (Tilquin 1942; Eberhard 1990).

The two patterns differed in that either the lines were laid without attachments to previously laid radial lines (A_1, A_2 in Fig. 8), or (more often) the spider attached its dragline one or more times to radial lines both on the way out and on the way back to the hub (B_1, B_2 in Fig. 8). Consecutive radial lines were always laid in different directions, as in orb construction by other araneoid spiders (Tilquin 1942; Dugdale 1969; Le Guelte 1966; Witt et al. 1968; Eberhard 1982). Each radial line was reinforced repeatedly, and the total amount of dragline silk in a cocoon web probably represented a major fraction of that in an orb. The estimated total numbers of radial lines in two finished cocoon webs were 36 and 30. Thus the number of radial trips was on the same order as the typical number of radii (20–35) in a normal orb (Fig. 1).

The behavior of one further individual, collected four days previously and observed in San Antonio de Escazu, was very different. The spider descended to the floor about 1.5 below the wire hoop, formed a "hub" where several lines converged about 1 cm above the floor, and then made 5–10 very long radial excursions (up to 1.3 m each) walking on the surface of the floor. As it moved away from the hub it walked in a nearly straight line, attaching its drag line periodically to the floor, but in some cases it gradually made an arc of up to more than 180° before it turned back and slowly retraced its path back to the hub. On at least four occasions the spider encoun-

Figures 6–7.—Dorsal view of an unusually elaborate cocoon web with hub loops and a frame line. Scale bars = 2.5 and 1.0 cm respectively.
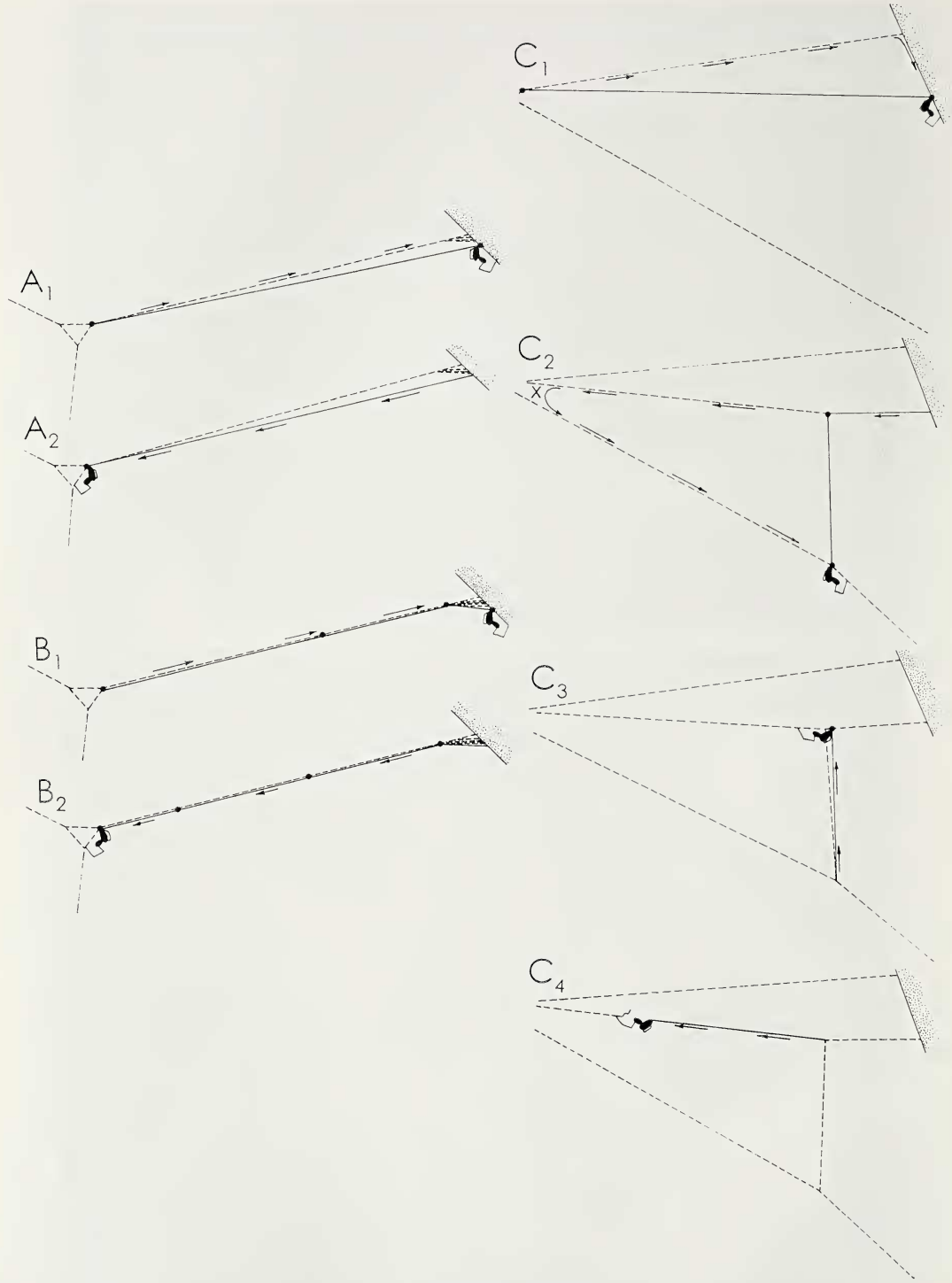
Figure 8.—Diagrammatic representations of the sequences of behavior during construction of a cocoon web (A_1–A_2, and B_1–B_2) and a frame line in a typical orb (C_1–C_4). Stippling represents substrate, black spots represent points where the dragline was attached, and dashed lines represent lines laid earlier in the sequence (C_1–C_4 after Eberhard 1990). Cocoon web construction corresponds to the behavior in C_1 and the first part of C_2.
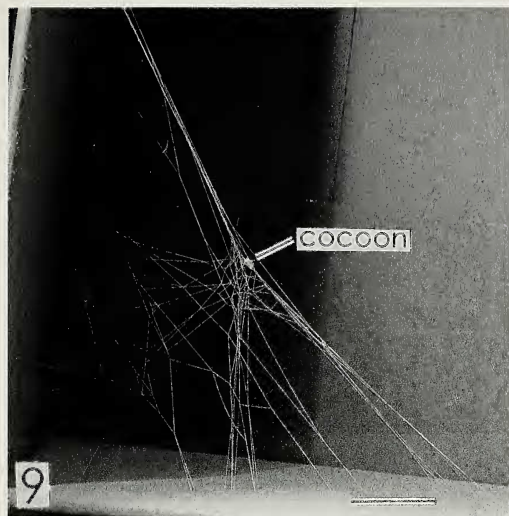
Figure 9.—Dorsal view of a web made by a mature male on the night that it was killed by a wasp larva. Note multiple attachments to substrate of some radial lines (as in Figs. 4 and 10). Scale bar = 3.0 cm.

tered an object that it could have climbed and thus have raised its drag line off the floor, but instead it struggled on across the floor. When I then removed the larva, and replaced the spider on the wire hoop after breaking the lines leading downward toward the floor, the spider again descended to the floor where it made another hub.

Wasps generally avoided parasitizing mature males (Eberhard 2000), but two larvae on mature males matured and made cocoons in captivity. One male spider did not make a cocoon web (or indeed any supporting structure whatsoever); the wasp's cocoon hung from a single short strand of spider silk. The second parasitized mature male spider, however, built an extensive web that resembled a cocoon web in being more or less planar, and having many attachments to the substrate on the night that it was killed and consumed by the larva (Fig. 9).

Experimental removal of larvae.—Larvae were removed from 22 spiders in captivity on the evening when the spider was to be killed. Four spiders built no webs that night. The 18 webs that were built were of three types. Three were more or less typical cocoon webs, with a low number of radial lines which were composed of multiple strands that were attached at many adjacent points on the sub-

strate, and more or less converged at the hub (Figs. 10, 11). A fourth spider, which had already begun cocoon web construction when I removed the larva, resumed cocoon web construction but did not return consistently to the hub, and made two additional "hubs". Simplified, "vestigial" webs, that had only a few more or less radial lines converging at the point where the spider rested and large masses of silk lines loosely packed together near the central area, were built by 13 spiders (Figs. 12, 13). These radial lines were attached to the substrate at only one or at most a few points. Vestigial webs never had hub loops, temporary spirals or sticky lines, and only seldom had recognizable frame lines. One further web was a nearly normal orb, except that the center of the hub was not removed and some portions of the sticky spiral lacked sticky balls.

The construction behavior of spiders from which larvae had been removed was observed for two cocoon webs and three vestigial webs. Cocoon web construction was very similar to that described above for spiders carrying larvae, including the frequent pauses between bursts of construction behavior, except that on some occasions the spider failed to attach its drag line at the hub when it returned after laying a radial line. The drag line laid on the next trip away from the hub was thus not attached at the hub, but originated part way out the previous radial line (line 2–4 in B_2 of Fig. 14). When this behavior was repeated over and over, the hub gradually expanded and became dispersed. The resulting web had large numbers of more or less radial lines attached to the substrate close to each other, but a diffuse central area (Fig. 15).

During vestigial web construction, the spider also made radial lines attached to the substrate just as above. On some return trips to the hub area, however, it broke and removed these lines, reeling them up and leaving them packed loosely together attached to the web. The final product of this process of repeatedly laying and then removing lines was a scanty array of more or less radial lines, and one or more large masses of fluff (Fig. 13).

None of the 22 experimental spiders that built webs died on the evening the wasp larva was removed. In nine cases the spider built a second web on the following night, and the second web was of the same type built on the
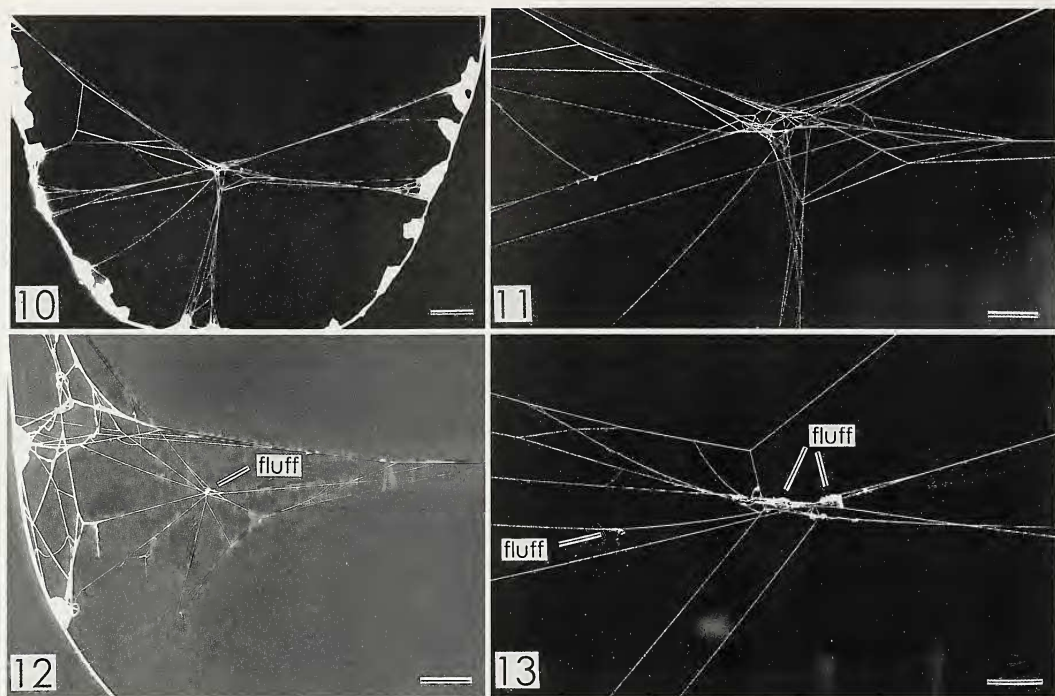
Figures 10–13.—Webs made by spiders from which the wasp larva was removed on the night when the larva would have normally killed the spider. 10. Cocoon-web type, in which the few radial lines each had multiple attachments to the substrate. Scale bar = 3.0 cm. 11. Close-up of hub of web in Fig. 10. Scale bar = 1.0 cm. 12. "Vestigial" type web, in which a few radial lines were attached singly to the substrate (heavy white lines are from previous web of another spider). Scale bar = 3.0 cm. 13. Close-up of the hub of a vestigial web (different web from that in Fig. 12), showing several masses of fluff. Scale bar = 1.0 cm; all wire hoops were horizontal.

first (two cocoon webs, seven vestigial webs). Five of the second vestigial webs had at least one hub loop. Due to deaths and emigrations, it was not possible to follow the spiders' behavior systematically on subsequent nights. Two spiders survived for a week, and gradually built webs that were progressively more orb-like though still substantially altered (Fig. 16).

DISCUSSION

Comparison of cocoon web construction behavior with the early stages of normal orb construction (Eberhard 1990) indicates that it is probably homologous with the early steps of type "D" frame construction (Fig. 8 C_1–C_4). Most anchor line construction in an orb involves removal of lines already in place, or shifting their attachments to each other (Tilquin 1942; Eberhard 1990), but neither of these behavior patterns was ever seen during cocoon web construction. In type D anchor

construction, however, which sometimes occurs as part of frame construction, the early stages do not involve removing or shifting lines (Fig. 8 C_1, C_2). Premature termination of this type of frame construction behavior when the spider returns to the hub after the first attachment to the substrate and followed by attachment of the spider's drag line at the central area (x in Fig. 8 C_2), would result in a sequence of operations identical to type A cocoon web construction (Fig. 8 A). Adding attachments to the line already in place on the way out would result in a sequence similar or identical to the second type of cocoon web construction behavior (Fig. 8 B). Similar attachments sometimes occur in the closely related L. mariana during frame construction of types "A" and "C" of Eberhard (1990) but were not seen in conjunction with type D of Eberhard (1990) (the same individual often performed more than one type while building a given orb). A further resemblance to attach-
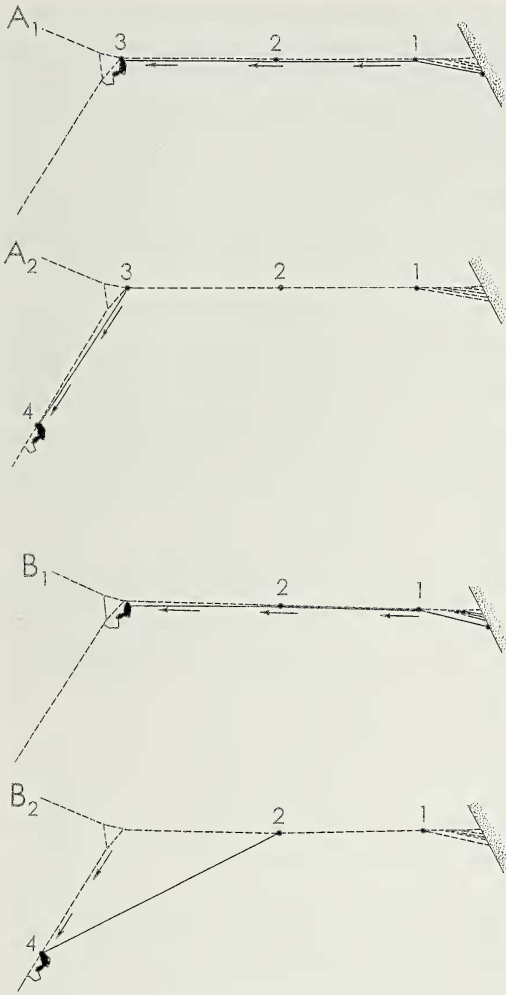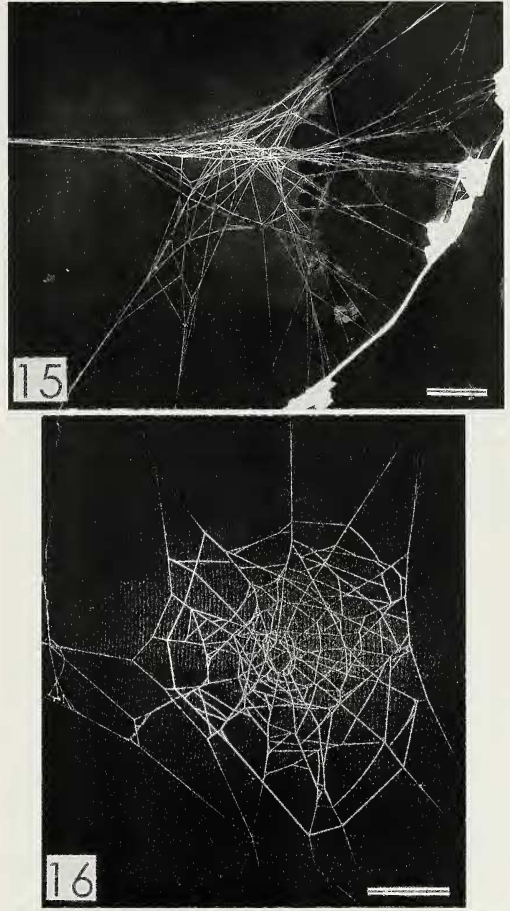
Figure 15.—Cocoon-type web with dispersed hub built by a spider from which the larva was removed on the evening on which it would have normally killed its host. Scale bar = 3.0 cm; wire hoop was horizontal.

Figure 16.—Orb-like web built by a partially recovered spider. The wasp larva had been removed five days earlier, on the evening when it would have killed the spider, and the spider had spun a typical vestigial web on that night. Scale bar = 2.0 cm.

Figure 14.—Diagrammatic representations of cocoon web construction behavior of a spider with a wasp larva (A_1, A_2) and a spider from which the wasp larva had been experimentally removed (B_1, B_2). The experimental spider sometimes omitted the final attachment at the hub typical of cocoon web construction (attachment 3 in A_1 and A_2; see also Fig. 8 A_2 and B_2); when it moved away from the hub to make the next radial line, the dragline was thus displaced away from the hub (line 2–4 in B_2). Repeated omissions of this attachment resulted in a diffuse central area of the web (Fig. 15).

ments of anchor lines built during orb web construction by other orb weavers (Tilquin 1942: Eberhard 1990) was the attachment of radial lines to thin objects by moving to the opposite side of the object just before attaching. Thus, the spider built the cocoon web by apparently repeating the first portions of one type of frame construction over and over. Fur-

ther evidence that cocoon webs were homologous with orbs is the fact that when these webs had more than three radial lines, these were nearly always in approximately the same plane. In addition, some cocoon webs had frame lines, and a few had hub loops (Figs. 6, 7).

The homology of cocoon and orb webs emphasizes that perhaps the most extraordinary aspect of the wasp larva's effect on the spider was not so much what the spider did, but what it did not do. Many aspects of normal orb con-

struction were completely absent, including both breaking, reeling up and replacing lines (e.g. Fig. 8 C_4), and breaking and then re-attaching lines. These two behavior patterns form integral parts of most types of both frame and radius construction in normal orbs of this and other species (Tilquin 1942; Eberhard 1982 1990; Coddington 1986). A single failure to repress these behavior patterns could be disastrous for the wasp larva, as it would result in the removal of the many-stranded cable of radial lines, and its replacement with a much weaker line. This indeed occurred in the vestigial webs built by spiders from which larvae were experimentally removed. Also completely missing were production of the temporary spiral and sticky spiral, and removal of the central portion of the hub at the end of orb construction, which again would have resulted in considerable weakening of the support for the wasp's cocoon. These differences between cocoon webs and normal orbs are appropriate to make the cocoon web stronger and less likely to be damaged by falling debris, and thus a more durable support for the wasp's cocoon than an orb would be. Strong support for the cocoon may be important for the wasp's survival, as in the related *Hymenoepimecis robertsae* some pupae died when heavy rains damaged cocoons (Fincke et al. 1990).

The importance of the precision of the behavior induced in the spider is also illustrated by the effect of occasional omission of one normal detail, the final attachment at the hub after a radial line was built (Fig. 8 A_2, B_2) that was seen in some spiders from which the larvae were experimentally removed. The resulting lack of a clear central point of convergence produced webs that were much less appropriately designed to support the wasp's cocoon (Fig. 15). It is not clear whether the aberrant behavior of one spider that laid radial lines on the surface of the floor instead of in the air was something that happens in nature (such webs would be missed in the field) or was an artifact of captivity.

In some cases, claims that modification of host behavior associated with parasitism represents an evolved adaptation by the parasite to promote its own reproduction have been controversial (Toft et al. 1991; Poulin 2000). There can be little doubt on this score with the species of this study, as the cocoon web

design is both unprecedented in *P. argyra* or any closely related orb weaver, and seems especially appropriately designed to increase the survival of the wasp. Induction of spinning behavior also occurs in several families of spiders parasitized by acrocerid flies; the spider spins a thin cell similar to that made just prior to moulting, and the larva clings to the web after emerging from the spider (Schlinger 1952, 1960, 1987).

The changes in the behavior of *P. argyra* are induced chemically rather than by direct physical interference with the spider's nervous system. The wasp larva contacts only the surface of the spider's abdomen and limits itself to making small holes through which it imbibes hemolymph (Eberhard 2000a,b). In addition, some spiders built normal cocoon webs after the larva was removed. Some ichneumonids modify host behavior and physiology via products injected by the female wasp when she oviposits (Gauld 1995). However, the lack of web modification in the days immediately following the attack by the wasp, the sudden abrupt shift in behavior that is coordinated with maturation of the larva, and the changes in webs produced by removing the larvae, all argue that the larva rather than the adult female wasp induced modified web construction behavior. Secretion of neuromodulators by parasitoid larvae has been implicated in behavioral changes produced in some insect hosts (Beckage 1997). The variety of web forms and construction behavior observed when the larva was removed prematurely suggest a complex, gradual effect rather than an abrupt, simple modification.

The ability of *Hymenoepimecis argyraphaga* to induce specific behavior patterns in spiders indicates that even these fine behavioral details are independent units or modules at some level within the spider, and not just artificial constructs. The additional web forms produced by experimentally removing larvae from spiders suggest even further subdivisions of building behavior. The problem of what constitutes a biologically realistic behavioral unit is crucial in the use of behavior patterns as taxonomic characters in orb-weavers Eberhard 1982; Coddington 1986, 1990; Scharff & Coddington 1997; Griswold et al. 1998) as well as in other animals (Wenzel 1992). The results of this study suggest that it is reasonable to attempt to use even finer behavioral

details than those that have been used previously in orb weaver taxonomy. The cocoon web of *P. argyra* is similar to the secondarily reduced "asterisk" web found by Stowe (1978) in the distantly related araneid *Wixia ectypa* (Walckenaer). Whether or not this evolutionary transition involved chemical changes similar to those produced by *H. argyraphaga* remains to be determined.

ACKNOWLEDGEMENTS

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